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DOI:

[10.1111/pala.12411](https://doi.org/10.1111/pala.12411)

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Peer reviewed version

*Citation for published version (Harvard):*

De Almeida Marsola, JC, Ferreira, G, Langer, M, Button, D & Butler, R 2019, 'Increases in sampling support the southern Gondwanan hypothesis for the origin of dinosaurs', *Palaeontology*, vol. 62, no. 3, pp. 473-482.  
<https://doi.org/10.1111/pala.12411>

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**Increases in sampling support the southern Gondwanan hypothesis for  
the origin of dinosaurs**

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**Abstract:** Dinosaurs were ubiquitous in terrestrial ecosystems through most of the Mesozoic and are still diversely represented in the modern fauna in the form of birds. Recent efforts to better understand the origins of the group have resulted in the discovery of many new species of early dinosaurs and their closest relatives (dinosauiromorphs). In addition, recent re-examinations of early dinosaur phylogeny have highlighted uncertainties regarding the interrelationships of the main dinosaur lineages (Sauropodomorpha, Theropoda and Ornithischia), and questioned the traditional hypothesis that the group originated in South Gondwana and gradually dispersed over Pangaea. Here, we use a historical approach to examine the impact of new fossil discoveries and changing phylogenetic hypotheses on biogeographic scenarios for dinosaur origins over 20 years of research time, and analyse the results in the light of different fossil record sampling regimes. Our results consistently optimize South Gondwana as the ancestral area for Dinosauria, as well as for more inclusive clades including Dinosauiromorpha, and show that this hypothesis is robust to increased taxonomic and geographic sampling and divergent phylogenetic results. Our results do not find any support for the recently proposed Laurasian origin of dinosaurs and suggest that a southern Gondwanan origin is by far the most plausible given our current knowledge of the diversity of early dinosaurs and non-dinosaurian dinosauiromorphs.

**Key words:** Dinosauria, sampling, biogeography, BioGeoBEARS, Triassic, Gondwana

DINOSAURS dominated Mesozoic terrestrial ecosystems for more than 140 million years, and remain highly diverse today, in the form of birds. As such, dinosaurs represent an outstanding example of evolutionary success among terrestrial tetrapods, which is reflected by the broad scientific interest in the group. Recently, there has been intense debate over the origins, early evolutionary radiation, and rise to ecological dominance of the group, stimulated by new discoveries of early dinosaurs and closely related taxa (Irmis *et al.* 2008; Nesbitt *et al.* 2009, 2010, 2013, 2017; Cabreira *et al.* 2011, 2016; Martínez *et al.* 2011), novel quantitative macroevolutionary analyses (Brusatte *et al.* 2008*a, b*; Sookias *et al.* 2012; Benton *et al.* 2014), and new geological data (Whiteside *et al.* 2015; Marsicano *et al.* 2016; Bernardi *et al.* 2018; Langer *et al.* 2018).

The discovery of many of the earliest known fossils of dinosaurs and their close relatives, non-dinosaurian dinosauiromorphs, in South America and other southern portions of the supercontinent Pangaea has led to the hypothesis that dinosaurs originated in this region (Nesbitt *et al.* 2009; Brusatte *et al.* 2010; Langer *et al.* 2010). However, a recent high-profile reassessment of the early dinosaur evolutionary tree (Baron *et al.* 2017*a*) not only challenged the long-standing classification of the three main dinosaur lineages (Seeley 1887; Gauthier 1986), but also questioned the southern Gondwanan origin of the clade. Based solely on the observed palaeogeographical distribution of some of the closest relatives of Dinosauria in their phylogenetic hypothesis (i.e., the Late Triassic *Saltopus elginensis* and the Middle–Late Triassic Silesauridae, which were recovered in a polytomy with Dinosauria), Baron *et al.* (2017*a, b*) proposed that dinosaurs may have originated in the northern part of Pangaea, referred to as Laurasia. However, this was suggested in the absence of any formal biogeographic analysis. Langer *et al.* (2017) tested this hypothesis by running several

quantitative biogeographical analyses to reconstruct ancestral areas, the results of which consistently recovered a southern Pangaeon (or Gondwanan) origin for dinosaurs. However, they only conducted these analyses for the Baron *et al.* (2017a) topology and did not consider alternative phylogenetic scenarios (e.g. Cabreira *et al.* 2016), or the long-term robustness of these results to new fossil discoveries.

In this paper we aim to: (i) further test hypotheses about the ancestral distribution of dinosaurs using a broader range of quantitative biogeographical models and alternative phylogenetic hypotheses; (ii) test the stability of the biogeographic results over 20 years of additional scientific discoveries and new research that have dramatically changed our understanding of early dinosaur evolution; and (iii) discuss how biased palaeogeographic sampling of the fossil record might impact our scenarios for dinosaur origins.

## MATERIAL AND METHODS

### *Source trees and time scaling*

We sampled trees from six independent phylogenetic analyses from the last 20 years, each of which dealt with the major diversity of early dinosauiromorphs at the time they were published: (1) Sereno (1999); (2) Langer and Benton (2006); (3) Nesbitt *et al.* (2009); (4) Cabreira *et al.* (2016); (5) Baron *et al.* (2017a); and (6) Langer *et al.* (2017) (Fig. 1). For the Baron *et al.* (2017a) dataset, we created three alternative topologies to explore the impact of the uncertain relationships between *Saltopus*, Silesauridae and Dinosauria found by that study. The three topologies differ in the following arrangements: A, *Saltopus* sister to Silesauridae + Dinosauria; B, *Saltopus* sister to

Silesauridae; and C, *Saltopus* sister to Dinosauria. We pruned Cretaceous taxa from the chosen topologies, as their biogeographical range is beyond the scope of our study. Supraspecific taxa were replaced by specific representatives of the same clade in order to generate a more explicit geographic distribution of terminal nodes. For example, in the topology of Sereno (1999) we replaced Diplodocidae with *Diplodocus*.

Since the biogeographic methods employed here require fully-solved, time-calibrated topologies, we resolved all polytomies in the sampled trees according to the following procedure. For hypotheses resulting from many most parsimonious trees (MPTs; e.g. (Langer *et al.* 2017)), we first obtained a majority-rule consensus tree (cut-off = 50). The remaining polytomies were manually resolved using a standardised procedure suggested by previous studies, e.g. (Upchurch *et al.* 2015; Ferreira *et al.* 2018). First, wherever possible we resolved polytomies to minimise biogeographic changes. For example, in a polytomy (*A,B,C*) where *A* and *B* share the same range, but *C* has a different range, we resolved *A+B* as sister-taxa to the exclusion of *C*. We further resolved polytomies based on relationships recovered in previous analyses. Finally, if polytomies remain, we chose the arrangement by randomly selecting one of the possible MPTs of that analysis. The dichotomous trees were then time-scaled using the R package *strap* (Bell and Lloyd, 2014), with branch lengths equally divided (Brusatte *et al.* 2008b), and a minimum branch length of 1 Ma. Time ranges were based on the oldest and earliest dates of the stratigraphic stage (according to the International Chronostratigraphic Chart v. 2017/02) in which a taxon occurs, the latter data being gathered from the literature. For example, the first and last appearances of all Carnian taxa were considered as 237 and 227 Ma, respectively.

*Biogeographical analyses*

In order to investigate the influence of phylogenetic uncertainty and sampling on ancestral distribution estimates for dinosaurs we conducted a series of stratified biogeographic analyses with the R package *BioGeoBEARS* (Matzke, 2013) using the aforementioned phylogenetic trees. For each analysis, we ran two nested-models (M0 and M1; see below) of the likelihood-based models DEC (Dispersal-Extinction Cladogenesis (Ree, 2005; Ree and Smith, 2008)) and DIVALIKE (Dispersal-Vicariance Analysis (Ronquist, 1997)) – DEC+J model was not explored because of its conceptual problems (Ree and Sanmartín, 2018). Even though *BioGeoBEARS* enables fitting a large number of additional models by changing the available parameters, e.g. the implemented likelihood version of BayArea (Landis et al., 2013), we opted to employ only the most commonly used biogeographic models, DEC and DIVA, to reduce the total number of analyses, since we are testing several sets of analyses based on different phylogenetic hypotheses. Each taxon was scored for four biogeographic provinces as defined by Langer *et al.* (2014): South Gondwana (S), Equatorial Belt (B), Euramerica (A), and Trans-Uralian domains (T). We set a maximum range size of two areas. Even though our analyses are temporally restricted between the Middle Triassic to Middle Jurassic, a period during which no drastic palaeobiogeographical changes between the considered areas are supposed to have occurred, we conducted time-stratified analyses dividing the trees into two discrete periods: Middle Triassic to Norian (247.2–208.6 Ma) and Rhaetian to Middle Jurassic (208.5 Ma to the earliest tip of each tree). For each time stratum a dispersal multiplier matrix was specified to model the arrangement between the defined areas. To compare the effects of these assumptions, we followed the procedure of Poropat *et al.* (2016) and conducted analyses with ‘*harsh*’ and ‘*relaxed*’ versions of the ‘*starting*’ dispersal multiplier matrices (Marsola *et al.* 2018,

[Appendix S1](#)), and also set the parameter  $w$  to be free in one of the models (M1; for M0  $w$  is set to 1), in order to infer optimal dispersal multipliers during the analyses. It is important to consider that distinct models (e.g., DEC and DIVA) make specific assumptions about the biogeographic processes of range change. For that reason, the maximum-likelihood approach of *BioGeoBEARS* allowed us to test and choose the best fit model (Matzke, 2014), using the likelihood-ratio test (LRT) and the weighted Akaike information criterion (AICc).

## RESULTS

With the sole exception of the ‘*starting*’ analysis of the Langer and Benton (2006) tree, for which a joint distribution of South Gondwana and Euramerica was estimated for the Dinosauria node, the best fit models (for LRT and AICc test results see [Marsola et al. \[2018\]](#), [Appendix S1](#) and [Supplementary Files](#)) obtained from all our analyses support a strictly southern Gondwanan origin for dinosaurs (Table 1). Changing the dispersal multiplier matrices did not yield distinct estimates. Similarly, our results yield high support for South Gondwana as the ancestral area for other ornithodiran clades leading to the Dinosauria node. Whereas all analyses of the Nesbitt *et al.* (2009) dataset and the ‘*starting*’ version of the Langer and Benton (2006) dataset support a joint distribution of South Gondwana and Euramerica as the ancestral area for Dinosauromorpha, the clades Dinosauromorpha and Dinosauriformes are supported as originating in South Gondwana in all other analyses, including in those datasets that have the most extensive sampling of non-dinosaurian dinosauriforms, (e.g. [Cabreira et al. 2016](#); [Baron et al. 2017a](#); [Langer et al. 2017](#)). South Gondwana is also inferred as the ancestral area for the Silesauridae + Dinosauria clade in all analyses in which this sister-group relation is



present (i.e. not in Sereno (1999) or iteration C of the Baron *et al.* (2017a) dataset), with the exception of the ‘harsh’ analysis of the Langer and Benton (2006) dataset. We note that the results for the Langer and Benton (2006) tree may not be reliable due to the low taxon sampling of the tree and the short branches surrounding Dinosauria.

Our results do not therefore support the hypothesis of a Laurasian origin for Dinosauria as proposed by Baron *et al.* (2017a), regardless of which of their three alternative topologies (Baron *et al.* (2017a): trees A, B and C) is employed. Although the problematic taxon *Saltopus elginensis* is known from Laurasia (Lossiemouth Sandstone Formation of Scotland, generally considered as late Carnian in age, and almost certainly Late Triassic; Benton and Walker 2011), it is phylogenetically nested among South Gondwana taxa in all alternative hypotheses and occurs stratigraphically 10–15 million years later than the main splitting events along the dinosauromorph lineage leading up to the origin of dinosaurs. Likewise, although Baron *et al.* (2017a) noted that the Laurasian *Agnosphytyx cromhallensis* was positioned as sister to other silesaurids in their results, this taxon is known from the Rhaetian fissure fill deposits of southwest England, i.e. some 35–40 million years after the inferred origin of Silesauridae. All known Middle Triassic non-dinosaurian dinosauromorphs, as well as the only putative Middle Triassic dinosaur (Nesbitt *et al.* 2013) are from South Gondwana and only from the Carnian onwards does their range expand into the northern hemisphere.

We conclude therefore, that the phylogenetic hypothesis proposed by Baron *et al.* (2017a) does not provide any significant support for a Laurasian origin of dinosaurs (Fig. 2). Instead, all our results strongly support those of Nesbitt *et al.* (2009) and Langer *et al.* (2017) (Fig. 2, 3), in which southern Gondwana (“southern Pangaea” and “South America”, respectively, in their own terms) was also recovered as the ancestral

area for dinosaurs. Furthermore, our analyses show that Ornithoscelida and Saurischia would also have originated in southern Gondwana in all possible versions of the Baron *et al.* (2017a) phylogenetic hypothesis.

**DISCUSSION**

*Historical patterns*

Palaeontologists frequently use ancestral-area reconstruction approaches, such as those implemented by *BioGeoBEARS*, to infer ancestral ranges for clades and use these to make inferences about evolutionary histories, e.g. (Upchurch *et al.* 2015; Poropat *et al.* 2016; Ferreira *et al.* 2018). However, they much more seldomly consider the robustness of those results to new fossil discoveries, which may include taxa from areas in which they were previously unsampled, and changes in phylogenetic hypothesis, which occur through the addition of more taxa and/or through changing topologies that result from new datasets or analytical approaches. For an ancestral range hypothesis to be considered well supported, it should be robust to such changes in the source data.

Here, we have provided a unique historical perspective on early dinosaur biogeography, by reconstructing ancestral areas for a series of alternative phylogenetic topologies taken from the last 20 years of research effort. Our key result – a South Gondwana origin for dinosaurs – has proved remarkably stable over two decades of new fossil discoveries and extensive phylogenetic research. Since the work of Sereno (1999), 23 new Triassic dinosaurs and non-dinosaurian dinosauromorphs have been discovered and/or added to phylogenetic studies. This included new taxa from North America (e.g. (Irmis *et al.* 2007; Nesbitt *et al.* 2009; Sues *et al.* 2011)), Europe (Fraser *et al.* 2002;

Dzik, 2003; Benton and Walker 2011) and North Africa (Kammerer *et al.* 2012). Yet, this greatly increased sampling has had few major impacts on models of early dinosaur biogeography, as the southern Gondwanan origin for the group is invariably supported as the best model throughout the research interval considered. We recommend using a similar historical perspective when estimating ancestral distributions of other clades, as a way of examining the support for biogeographical hypotheses.

Our results are also consistent despite highly divergent phylogenetic hypotheses for early dinosaurs. For example, Cabreira *et al.* (2016) recovered the majority of silesaurids within Dinosauria, as a paraphyletic array of early ornithischians. Baron *et al.* (2017*a, b*) proposed the unconventional clade Ornithoscelida, with Ornithischia as the sister-taxon of Theropoda, and herrerasaurids nested with sauropodomorphs within Saurischia, whereas Langer *et al.* (2017) reiterated support for a traditional Ornithischia-Saurischia dichotomy at the base of Dinosauria. However, our results show that none of these conflicting rearrangements of the three main dinosaurian lineages (Sauropodomorpha, Theropoda, Ornithischia) and Silesauridae challenge the long-standing biogeographic hypothesis of a southern Gondwanan origin for dinosaurs.

### *Sampling biases*

A biogeographic hypothesis, such as the southern Gondwanan origin of Dinosauria, may be well supported through research time and under alternative phylogenetic topologies, but could still be flawed if fossil record sampling is highly heterogeneous. For example, if dinosaurs actually originated in the late Middle–earliest Late Triassic in Laurasia, and dispersed quickly across the globe, they might still be reconstructed as ancestrally from South Gondwana if that region is the only one from which terrestrial

vertebrate fossils have been sampled in that time interval. Reconstructions of ancestral areas for fossil taxa should therefore always be considered within an explicit consideration of how the fossil record has been sampled spatially, and temporally, but this is rarely the case. Here, we briefly discuss fossil record sampling through the inferred origin and initial radiation of dinosaurs (Middle Triassic–early Late Triassic: Anisian–Carnian), and the implications for the South Gondwana origins hypothesis.

The earliest dinosauiromorph body fossils, as well as the oldest putative dinosaur body fossil, are known from the Middle to earliest Late Triassic of South Gondwana, most notably from the Manda Beds of Tanzania (Nesbitt *et al.* 2010; 2013; 2017) and the Chañares Formation of Argentina (Serenó and Arcucci 1994*a, b*; Bittencourt *et al.* 2015; Ezcurra *et al.* 2017) (Fig. 4). These represent two of the best-sampled stratigraphic units for terrestrial tetrapods in this interval, but Laurasian tetrapods of broadly comparable stratigraphic ages are known from various Laurasian localities, including the USA (Moenkopi Formation; e.g. Nesbitt (2005)), the UK (Helsby Sandstone Formation; e.g. Coram *et al.* (2018)), Russia (Donguz and Bukobay gorizonts; e.g. Gower and Sennikov (2000)), Germany (Erfurt Formation; e.g. Schoch and Sues (2015)) and China (Ermaying Formation; e.g. Sookias *et al.* (2014)). To date, none of these Laurasian deposits have yielded dinosauiromorph body fossils (Fig. 4).

Similarly, the earliest definitive dinosaur body fossils are from the early Late Triassic (late Carnian) of Argentina and Brazil (Alcober and Martínez 2010; Brusatte *et al.* 2010; Ezcurra 2010; Langer *et al.* 2010; Cabreira *et al.* 2011; 2016; Martínez *et al.* 2011; Müller *et al.* 2018; Pretto *et al.* 2018) (Fig. 4). Although the dating of many Laurasian rock sequences of putatively similar age is controversial, those in Germany (e.g. Butler *et al.* (2014)), Poland (e.g. Dzik and Sulej (2007)), North America (e.g. Sues and Olsen (2015)), and the UK (e.g. Benton and Walker (1985)), have failed thus

far to yield definite dinosaur remains, although the silesaurid *Silesaurus* is known from Poland (Dzik 2003), and the problematic *Saltopus* from the UK (Benton and Walker 2011).

Putative dinosauiromorph footprint records have been reported from the Early–Middle Triassic of Laurasia (Brusatte *et al.* 2011). These include the ichnogenus *Prorotodactylus* from the Olenekian of Poland (Brusatte *et al.* 2011; Niedźwiedzki *et al.* 2013) and the ichnogenus *Rotodactylus* from the late Olenekian–Ladinian of Poland, Germany, France, the UK and the USA (Peabody 1948; Haubold 1999; Brusatte *et al.* 2011; Tresise and King 2012; Niedźwiedzki *et al.* 2013). If this interpretation of trackmaker affinities is correct, it represents a significant challenge to current understanding of the biogeography of early dinosauiromorphs (although not necessarily dinosaurs), suggesting that they were widespread over northern Pangaea in the late Early–Middle Triassic. However, trackmaker affinities for footprint ichnogenera are often difficult to constrain, and other workers have challenged the identification of *Prorotodactylus* and *Rotodactylus* as dinosauiromorphs (e.g. Padian 2013), suggesting that they could instead represent basal archosauiromorph or lepidosauiromorph trackways.

In order to test the effects of the possible dinosauiromorph affinities of the above-mentioned ichnogenera for dinosauiromorph and dinosaur biogeography, we performed sensitivity analyses with *Prorotodactylus* added to the Baron *et al.* (2017: tree C) and Langer *et al.* (2017) datasets (see Marsola *et al.* 2018, Appendix 1 and Supplementary Files). To do this, we considered two alternative possible scenarios where *Prorotodactylus* is sister-taxon to all other dinosauiromorphs, or is sister-taxon to all lagerpetids. Invariably, the results (Marsola *et al.* 2018, Appendix S1) consistently continue to infer South Gondwana as the ancestral area for both Dinosauria and

Dinosauriformes. On the other hand, a joint distribution of South Gondwana and Euramerica as the ancestral area for Dinosauromorpha is supported in most cases, although some analyses also suggest a joint distribution of Equatorial Belt and Euramerica.

It remains possible that, as suggested by Baron *et al.* (2017*b*), better future sampling of Middle–early Late Triassic localities from Laurasia will overturn the South Gondwana hypothesis for dinosaur origins. However, compared to those from South Gondwana, these areas have been much more extensively sampled by palaeontologists for >150 years and have so far failed to yield body fossils of Middle Triassic dinosauromorphs or early Late Triassic dinosaurs.

CONCLUSIONS

The last two decades have witnessed a great increase in the taxonomic sampling of Triassic dinosaurs and non-dinosaurian dinosauromorphs. Unearthed from different parts of the world, these new discoveries have helped palaeontologists to better understand not only the morphology and diversity of early dinosaurs, but also to develop new models for their rise. Along with these new finds, new phylogenetic hypotheses for early dinosaurs have been proposed. These have challenged conventional understanding of the relationships of the main dinosaurian lineages (e.g. Cabreira *et al.* (2016); Baron *et al.* (2017*a*); Langer *et al.* (2017)), and questioned the long-standing hypothesis of a southern Gondwanan origin for the clade (Baron *et al.* 2017*a*; Langer *et al.* 2017). In this study, we have shown that even in the most divergent phylogenetic hypotheses of early dinosaurs, a southern Gondwanan origin is strongly supported by

quantitative biogeographic analyses. Additionally, we have demonstrated that South Gondwana is consistently supported as ancestral area in a range of phylogenies from the last 20 years, and has therefore been robust to increases in taxonomic, geographic and phylogenetic sampling. Although Middle–Late Triassic rock sequences worldwide have been sampled for decades, the oldest unequivocal dinosaur body fossil remains are still clustered in southern Gondwanan deposits. Given the present data, the South Gondwana hypothesis must therefore be considered the best-supported interpretation of the ancestral area for the rise of dinosaurs.

*Acknowledgements.* We thank Paul Upchurch for providing training in the use of *BioGeoBEARS*. This research was funded by the São Paulo Research Foundation (grants 2013/23114-1 and 2016/02473-1 to JCAM; 2014/25379-5 and 2016/03934-2 to GSF; 2014/03825-3 to MCL). RJB was supported by a Marie Curie Career Integration Grant (630123). **The editor Roger Benson, Sally Thomas, and the referees Steve Brusatte and Martin Ezcurra are deeply thanked for their suggestions which greatly improved the final version of this manuscript.**

*Authors' contributions.* RJB conceived the study. JCAM collected data. JCAM, GSF, and DJB conducted analyses. JCAM, GSF and RJB wrote the paper. All authors revised and contributed comments to the final manuscript.

*Competing interests.* We declare no competing interests.

## DATA ARCHIVING STATEMENT

R scripts and data for the biogeographic analyses are available in the Dryad Digital Repository.

<https://datadryad.org/review?doi=doi:10.5061/dryad.6t5m946>

**SUPPORTING INFORMATION**

Additional Supporting Information (Marsola *et al.* 2018, Appendix S1 and Supplementary Files) can be found in the online version of this article.

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## FIGURE CAPTIONS

FIG. 1. Three phylogenetic topologies of early dinosaurs, showing the increased taxonomic and phylogenetic sampling of taxa since 1999. A. Sereno (1999). B. Langer and Benton (2006). C. Langer *et al.* (2017). Names in blue represent Jurassic taxa. Names in green represent taxa discovered from 1999–2009. Names in red represent taxa discovered from 2010–2017.

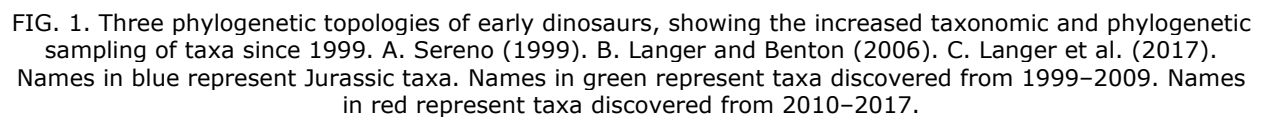
FIG. 2. Ancestral area reconstruction for the time-calibrated tree of the best biogeographical model of the ‘starting’ version of Baron *et al.* (2017a: topology C) (DIVA M0). Pie charts depict the probabilities for ancestral areas of nodes. Rectangles next to the taxa indicate their temporal range and the colours indicate their area.

FIG. 3. Ancestral area reconstruction for the time-calibrated tree of the best biogeographical model of the ‘starting’ version of Langer *et al.* (2017) (DIVA M1). Pie charts depict the probabilities for ancestral areas of nodes. Rectangles next to the taxa indicate their temporal range and the colours indicate their area.

FIG. 4. Palaeogeographical distribution in continental deposits of non-dinosauromorph Tetrapoda, non-dinosaur Dinosauromorpha and Dinosauria during the (A) Middle Triassic/early Carnian and (B) late Carnian.

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Table 1. Best fit models for each analysed tree. All results are available in Marsola *et al.* (2018, Appendix S1).



## Palaeontology

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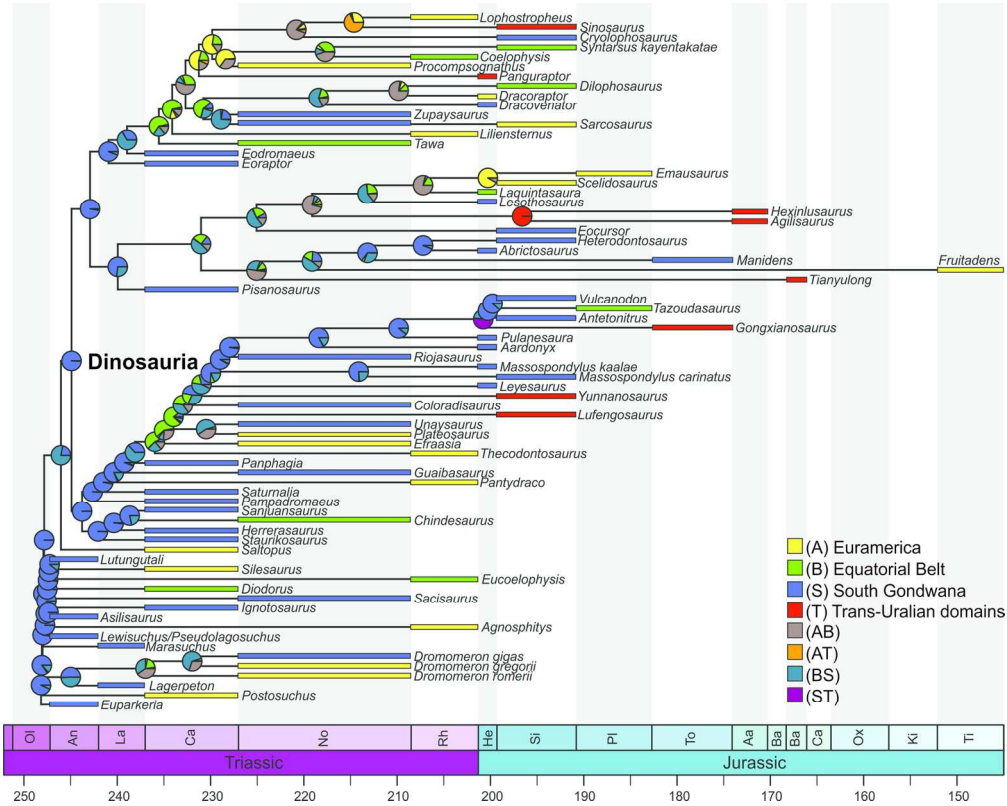


FIG. 2. Ancestral area reconstruction for the time-calibrated tree of the best biogeographical model of the 'starting' version of Baron et al. (2017a: topology C) (DIVA M0). Pie charts depict the probabilities for ancestral areas of nodes. Rectangles next to the taxa indicate their temporal range and the colours indicate their area.

156x124mm (300 x 300 DPI)

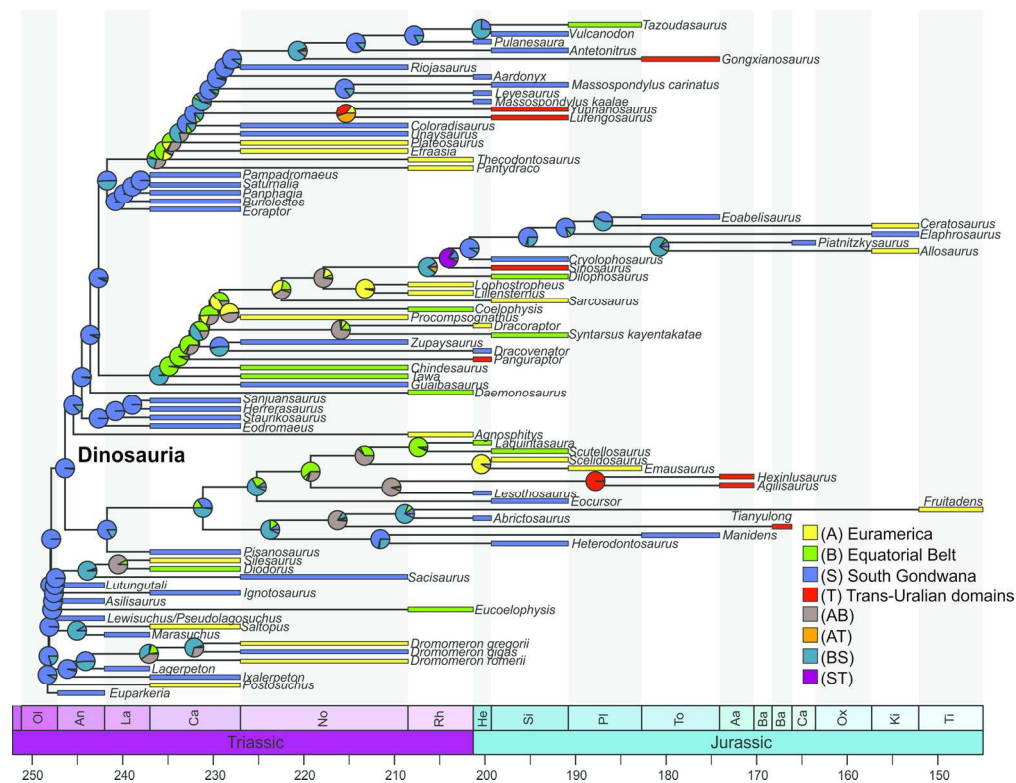


FIG. 3. Ancestral area reconstruction for the time-calibrated tree of the best biogeographical model of the 'starting' version of Langer et al. (2017) (DIVA M1). Pie charts depict the probabilities for ancestral areas of nodes. Rectangles next to the taxa indicate their temporal range and the colours indicate their area.

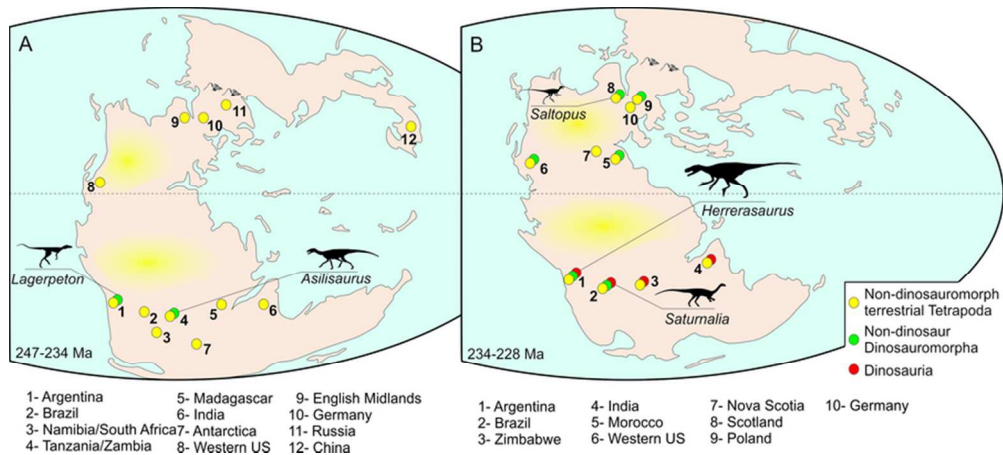


FIG. 4. Palaeogeographical distribution in continental deposits of non-dinosauriform Tetrapoda, non-dinosaur Dinosauriforma and Dinosauria during the (A) Middle Triassic/early Carnian and (B) late Carnian.

76x34mm (300 x 300 DPI)

Tree	Distance multiplier	Best model	Ancestral Area for Dinosauria
Sereno, 1999	Starting	DIVA M1	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana
Langer & Benton, 2006	Starting	DEC M0	South Gondwana and Euramerica
	Harsh	DEC M1	South Gondwana
	Relaxed	DEC M1	South Gondwana
Nesbitt et al., 2009	Starting	DEC M0	South Gondwana
	Harsh	DEC M1	South Gondwana
	Relaxed	DEC M0	South Gondwana
Cabreira et al., 2016	Starting	DIVA M0	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M0	South Gondwana
Baron et al., 2017 A	Starting	DIVA M1	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana
Baron et al., 2017 B	Starting	DIVA M1	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana
Baron et al., 2017 C	Starting	DIVA M0	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana
Langer et al., 2017	Starting	DIVA M1	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana